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THE DEVELOPMENT OF VEGETATION IN THE MORAINAL DEPRESSIONS OF THE VICINITY OF WOODS HOLE.

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(WITH SIX FIGURES)

FEW regions afford better opportunity for observing the stages in the history of small swamps than the vicinity of Woods Hole, Mass. The land of the neighborhood, a few outcrops of Cretaceous strata excepted, consists of the eroded mass of a terminal moraine. Clay, sand, and fragments of stone grading up to huge boulders constitute the country rock. Indenting the surface of this mass of *débris* are innumerable specimens of the peculiar depressions known to geologists as "kettle holes." In such hollows ponds and lakes have formed, each one the first term of a long series ending in its own obliteration. The changes by which the pond is destroyed, and in which vegetation plays so important a part, furnish a subject of absorbing interest. Many workers have gone far toward giving us an understanding of such a history. However, our knowledge is not complete, and questions which arose in the work at the Marine Biological Laboratory have led to this attempt to answer them. The present paper may be conveniently divided into three sections.

PHYSICAL FACTORS—EROSION AND DEPOSIT.

The authors who have pointed out the interesting and important part played by vegetation in the filling of ponds have possibly minimized the purely physical factors. At times the latter play a leading, and at times, as in cases mentioned later, an exclusive part.

The amount and the character of the silt washed down varies greatly with the nature of the surrounding surface. Where the latter has been disturbed by man, the quantity of material brought in, even by summer rains, is often astonishing.

Fig. 1 shows a pond in the edge of the village, adjoining a road. On July 2 there was a thunder shower lasting for about an hour. During that time a deposit was formed at one corner of this pond some 25^{sq. m} in area and 30–90^{cm} in depth. Four weeks later came another, less violent shower. The surface of the first deposit was cut down part way across by 40–50^{cm}, and



FIG. 1.—Pond in edge of village.

the material, aggregating many tons, borne farther out. The obliteration of this pond within two or three years may be expected. Of course, we are here dealing with highly disturbed conditions, but nevertheless the case may serve to enlarge our ideas as to the rapidity with which silt may be moved down. During the early period immediately following the retreat of the glacier, and before vegetation gained a footing, deposits in these depressions must have been made with enormous rapidity.

Where the pond is surrounded by grassy fields, the washing-in process is much restricted. That it still goes forward, however, one need only examine the pond margin to learn. A zone

of fine earth and sand encircles the pool, pushing slowly inward. If the contour of the surrounding land is such that the rain rivulets cut out a gully, the zone of silt deposit opposite its mouth indents the pond as a sandy or gravelly delta. These borders and deltas of silt become the seat of well-marked plant societies. *Gratiola aurea* in particular occurs with regularity, and its yellow blossoms may indicate to the eye at a distance the limits of such deposits. If the pond is situated in the deep woods, results are produced which are apparently paradoxical, and will be discussed below.

NOTES UPON SUCCESSIVE STAGES.

Large holes present, of course, the earliest phases, and in the small ones the more advanced conditions are found. As a type of the former we may chose Long pond, near Falmouth village. It is about $2\frac{1}{2}$ kilometers long, and reaches a depth of 28 meters. The shores are of the usual morainal materials, and in some places precipitous. As usual in such cases, it is without drainage, yet its depth and area are such that its water is well aerated, and, as analyses have shown, is nearly free from organic matter. The scanty vegetation admits of being described with some exactness. In the body of the pond no plants are seen. Near the shore appear some filamentous algae, and four species of flowering plants. The latter are distributed in two zones, sharply and surprisingly separated by one destitute of vegetation.

Limnanthemum lacunosum forms a continuous belt, but one which *never touches the shore line*. Soundings taken all around the lake show that the *Limnanthemum* zone is here confined to water between 0.6 and 3.9^m in depth. These soundings were made in August, when the water was about 20^{cm} lower than the line seen on the rocks. *Limnanthemum*, then, is here able to anchor on the bottom and float its leaves in water somewhat exceeding 4^m in depth. *Lobelia Dortmanna* appeared in about the same zone, growing entirely submerged, and could be seen from the surface through the transparent water. For obtaining specimens a bathing suit was useful. Many of the plants had put forth long scapes

at the time, but these could not reach the surface, and the blossoms decayed without opening. Like the preceding species, this did not occur in the shallow water next the shore line. *Gratiola aurea*, in its strictly hydrophilous form, was found in company with these also, but did not appear to flourish.

Between the zone of these three plants and the shore line was a space of open water, devoid of phanerogamic vegetation.

On the shore line, its roots submerged, *Euthamnia* (*Solidago*) *graminifolia* appeared, and its rich border of bloom nearly circumscribed the pond. That the zone of *Limnanthemum* and *Lobelia* did not extend inward till met by *Euthamnia* seemed a circumstance needing explanation, especially since both the former flourish elsewhere in very shallow water.

At some points wave-marks on the bottom had been seen, and it was noticed that the outer limit of these coincided with the shoreward limit of the *Limnanthemum* zone. Sandy silt in some quantity was coming in from the surrounding slopes. *Limnanthemum* plants along the shoreward margin of the zone were found buried in sand at the bottom, and dying. There seemed then reason for believing that the shoreward limit of this zone was set by the action in shallow water of the wavelets in shifting the silt, and burying the bottom growing vegetation.

Fig. 2 is a graphic illustration of action of this sort, drawn from a large pond on an adjacent island, called West end lake. Silt is coming into the pond from the low surrounding hills. At one spot a great boulder, out from the shore line, breaks the wavelets, and the silt has run out to it as a sandy peninsula whose curving sides represent the hyperbola of the broken wave action. Thus the outlying boulder plays a rather fantastic part in the growth of the land, and shelters a certain area from the smothering action of material which comes from the shore. The nearly clean, sandy bottom of the margin of this lake is due to the fact that the shallow water vegetation is constantly overwhelmed by the encroaching silt. Sheltered behind the boulder, a colony of *Juncus militaris* is growing.

At Long pond, *Euthamnia*, nevertheless, grew just at the

shore where the danger of burial was greatest. Explanation of this fact was found by digging, for the plant possessed running stems, penetrating the sand in all directions in a manner similar to sand binders, and like them was able to grow out as fast as buried. *Limnanthemum* and *Lobelia* have no runners, and so are driven to the zone beyond.

At the south end of Long pond, the slopes surrounding are of

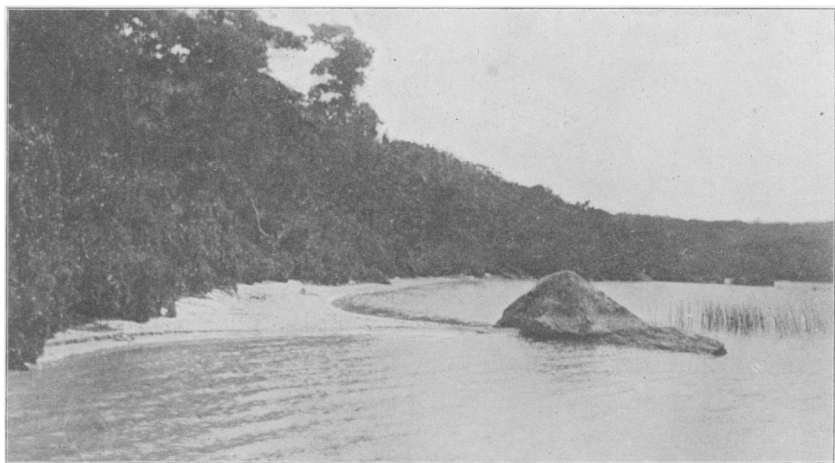


FIG. 2.—West end lake.

such a contour that washings would be swept toward a certain portion of the shore line. Moreover, the surface near this portion has been broken by cutting a road, and silt is brought in great quantities. Where this material reaches the shore line a sandy beach is formed, and from the beach it has advanced into the pond some 30 meters as a submerged delta. The diagram (*fig. 3*) may aid in making the case clear. The outline of the delta is shaded; the sandy beach represented by the line *a-b*. Now the *Limnanthemum-Lobelia* zone (indicated by the small circles) follows closely the outline of the submerged delta, and the *Euthamnia* zone on the shore (outlined by the scroll) is interrupted by the sandy beach. The fact is that the former

zone is driven outward by the advancing silt, and the latter interrupted altogether, despite the running stems of *Euthamnia*. Rowing around above the edge of the delta, and looking down through the transparent water, one can see colonies of *Lobelia* growing in the little hollows around the margin of the deposit.

If the latter should advance, the fate of these colonies is easy to predict.

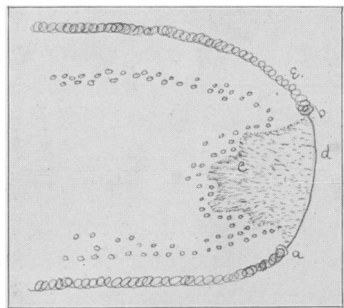


FIG. 3.—Diagram of south end of Long pond.

Fig. 4 is from a photograph taken from *c*, and including the shore line from *d* to *e*. From *d* to *b* may be seen the sand beach, from *b* to *e* a portion of the *Euthamnia* zone, which continues unbroken a kilometer or more from that point.

Somewhat more advanced than that of Long pond is the stage of a pond near by. The latter is smaller, and analyses here show a considerably greater proportion of organic matter. Portions are shallow, and in such *Nuphar* and *Pontederia* are making dense beds. Along the margin *Euthamnia* finds the space disputed by *Lysimachia stricta*, *Lycopus*, and *Coreopsis roseus*. Running subterranean stems are possessed by all these plants, and they are able to defy burial by silt in moderate quantities.

The history of the destruction of the shallow pool has been often described. The encroaching of the plants from the margin, the increase of such plants as *Nuphar* and *Nymphaea* in the body of the pool till a footing is afforded for less anchored forms, and the consequent formation of the floating mat, may be here passed over with a few local notes. All stages may be splendidly seen in this region. Among recollections of the summer are vivid ones of trying to reach attractive patches of *Xyris* or *Drosera* in bloom, and learning that the apparent ground was only floating mat with ominous depths below.

Nuphar and *Nymphaea* take an important part in the first

formation of the floating vegetation. When a pond happens to be of nearly uniform depth, of 1^m or less, *Nymphaea* may grow in a luxuriance almost incredible. In such a pool, perhaps 150 meters in diameter, near Succoneset point, water lilies were growing and blooming in such profusion that when it was found in July the surface of the pond seen through the trées gave the



FIG. 4.—South shore of Long pond.

effect of an unbroken sheet of white. *Limnanthemum* and *Brasenia* are in some cases important constituents of the first pond vegetation.

In certain places *Hypericum boreale* takes a leading part. This plant shows an interesting dimorphism. It grows submerged as a sparingly leafy unbranched axis, weak and slender, erect by its own buoyancy. When it reaches the surface, however, it breaks out into a strong branching herb, sustaining masses of aerial foliage from enlarged stems floating horizontally on the surface. At Flax pond, in about 30^{cm} of water, it forms thus continuous floating masses many square meters in area.

When such anchored forms, especially the strong ones like Nuphar, gain a good footing, the floating mat vegetation follows apace. Several species of *Utricularia* aid greatly in this process, by means of their floating and branching tufts. *Sphagnum* and other mosses, *Carices*, *Xyris*, and *Drosera* appear.

In still further building the mat, and in giving it firmness, *Decodon verticillatus* plays a leading part. Several adaptations give it its preeminence, namely, the firmness of its woody roots and stem bases; its ability, nevertheless, to grow almost floating, only slight support being necessary; and its power of propagating from the tips of its shoots wherever they touch the water. The woody parts mentioned are clothed with thick layers of aerenchyma. Probably this tissue is not only a means of respiration, but also of importance in floating the plant. *Decodon* occurs almost universally in the yielding ponds.

We have seen that in Long pond, an open lake, the vegetation is purely hydrophilous. About the time of the formation of the floating mat, the general conditions rapidly become xerophytic. Following *Decodon*, and finding footing on its stools, appear a host of xerophilous shrubs. *Clethra alnifolia*, *Azalea viscosum*, *Vaccinium corymbosum*, *Ilex verticillata*, *Myrica cerifera* and *M. Gale*, *Andromeda ligustrina*, *Leucothoe calyculata*, sometimes *Cassandra* and others, rapidly transform the floating mat into a swamp thicket. It is observable that these shrubs, though representing widely different alliances, have a certain common facies. All have alternate, simple, lanceolate, nearly entire and nearly smooth leaves.

Decodon passes away before the shrubs, and in due time seedlings of trees begin to appear. As these trees, often wholly *Chamaecyparis*, grow, the shrubs are overtopped and yield, and the series enters a final cycle as a *Chamaecyparis* swamp.

Three such swamps in the immediate vicinity of Woods Hole afford beautiful illustrations of these final stages. For the sake of description we may designate them as *x*, *y*, and *z*.

In *x* the water still stands for most of the year between the stools. *Chamaecyparis* trees, 10–25^{cm} thick, rise from these

stools, and only close to their bases may the visitor here find footing. Clumps of *Vaccinium corymbosum* and *Leucothoe* show that these shrubs survive shading better than the other members of the bygone thicket. Between the trees a rod may be thrust

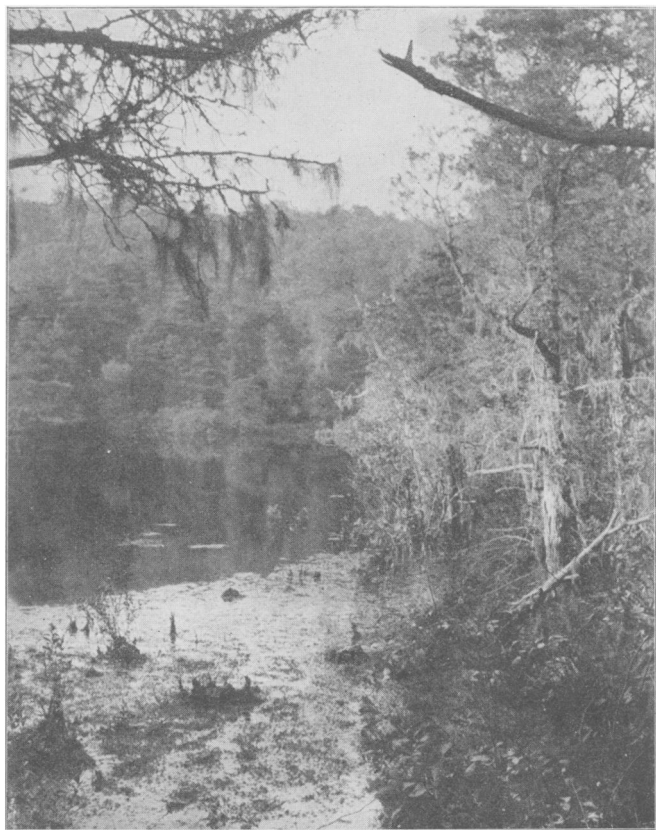


FIG. 5.—*Chamaecyparis* swamp.

down 5 meters without touching bottom. If one succeeds in making his way to the center, he finds a deep and dark pool perhaps 50 meters in diameter, of whose appearance some idea may be gained from *fig. 5*. On its surface is no vegetation, except a border clinging to the spreading roots of the trees. Long

tufts of *Usnea barbata*, simulating *Tillandsia usneoides*, hang from the trees, and if the beholder is of an imaginative disposition, the weird scene becomes for him a recess of some sub-tropical swamp.

In γ the water is less in evidence, and sometimes disappears from the surface for many weeks during the summer. The trees average slightly larger. In depressions between their stools Sphagnum is growing; on the stools themselves, thick cushions of other mosses. Shrubs are nearly absent, the lower portions of the trees' trunks are branchless, and one looks through sombre forest aisles, darker and more still than those of a pine forest. No pool is found at its center; matters have gone farther here, and the encroaching vegetation has covered the one time pond completely over.

In swamp α water is ordinarily absent, and the ground is firm enough that one may walk where he will. The trees are noticeably larger, some reaching a diameter of 45 cm. *Osmunda cinnamomea* grows in abundance. Young cedar trees are scarcely found, and one realizes that he beholds the penultimate term of the long series.

THE ORIGIN OF POND-ISLANDS AND ATOLLS.

In frequent instances the filling-up of the pond takes place in a fashion seemingly paradoxical. Instead of the deposit gradually encroaching from the margin, an island forms in the center and leaves a narrow belt of open water about the edge of the pool.

Fig. 6 shows a case of pond perhaps 15 meters in diameter, near Quisset harbor. That a pond should begin by filling up in the middle is a fact calculated to arouse the curiosity of a layman. The sharpness of the ditch and the frequency with which it appears call for an understanding of its origin. Perhaps it is the same as described by MacMillan¹ in connection with "plant atolls." Yet the hypothesis put forth in the paper cited seems scarcely applicable to the present cases.

¹ On the occurrence of Sphagnum atolls in central Minnesota. Minnesota Botanical Studies 1: no. 9. 1894.

If the pond were larger and deeper than the one shown in *fig. 6*, a pool would remain in the center and we should have a ring of vegetation between the ditch and the central pool. Indeed there is at least one such veritable atoll in the vicinity at present in question, and it is found in a larger basin, perhaps 100 meters in diameter.

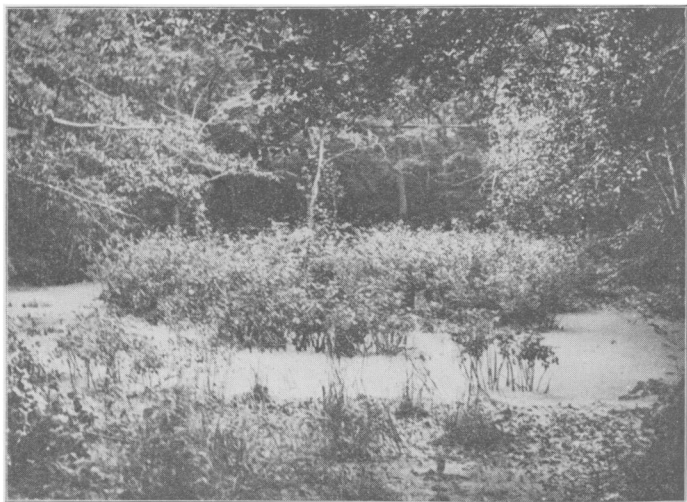


FIG. 6.—Pond-island near Quisset harbor.

The view is here taken that this atoll at least differs from a pond-island only in the fact that a larger kettle-hole is involved, and that in consequence a ring of vegetation is formed instead of an island. The problem would then resolve itself into accounting for the marginal ditch.

Professor MacMillan suggests that the ditch owes its origin to a fall and subsequent rise in the water level of the pond, and the spreading of the water beyond its one time boundaries. In the present cases some facts seem to call for more explanation than this hypothesis affords. The ditches, though perfectly sharp, are quite shallow, having an average depth of about 70^{cm}. Promising territory as this would be, aquatic plants showed little disposition to invade it. An artificial excavation of any sort is

generally soon seized upon, and the fact that these marginal ditches remain devoid of vegetation, not being even bordered with the usual water margin plants, suggested to the writer that there must be some cause which prevents the growth of vegetation in that zone, and that this might be identical with the one which originally gave rise to the ditch. A rise of water, in conjunction with such a cause, might make a compound atoll.

Atkinson, in his *Lessons in botany*, makes additional suggestions in regard to the origin of the ditch, one of which is that it is caused by the shade of trees and shrubs growing on the solid land, and thus giving low vegetation around the border of a pool a poor opportunity. However, the northern edge of a pond is quite exposed to the sun during the hours of midday, yet the ditch exists there as markedly as anywhere else.

It was observed that formations of this character were found only in wooded districts, or on those recently cleared. Portions of the islands of the neighborhood are treeless, and in these localities the ponds were filling up from the margin in the well known manner.

Another fact was eventually noticed, namely, that the ditch varied in width, and that this variation bore a constant relation to the contour of the surrounding surface. The ditch is always widest where, from the arrangement of the surrounding slopes, the most material is washed in. That fact seemed to harmonize ill with ideas of erosion and deposit.

When the character of the material brought in was considered, however, an explanation of the different facts began to appear. The forest floor around is of humus, and covered with a close felt of roots, mosses, and mycelia. It does not take a long examination to convince one that ordinary erosive action of rain has literally ceased. Only fallen leaves and other organic matter is washed into the pond. Such is brought in, however, in quantities, and young plants which might start around the edge are constantly smothered. The bottom of the ditch may be seen always covered with quantities of dead leaves; and reaching into the water one can grasp great handfuls in all

stages of decay. New material, brought in with every shower, adds to the decaying mass, and produces a zone nearly destitute of growing plants, widest where the washings of the forest floor are most swept in.

Organic material, unmixed with sand or earth, in decaying forms solid strata very slowly. A considerable period must elapse before this zone is filled up. Even the detritus thus slowly formed may not remain at the margin, *for the island of vegetation is a floating one*, and the real bottom of the pool is more or less basin shaped. The islands are in fact floating mats, and are likely to afford only a very doubtful footing, but by felling a tree upon one somewhat smaller than the one shown, it was possible to reach the center and learn that in that case there are 2 or 3 meters of water in the center on which the floating island rests. The detritus resulting from decomposition of matter in the marginal ditch slides into the deeper parts of the pool, and thus the stage of the ditch is yet more prolonged. After the island becomes fixed, the ditch still fills very slowly. Even after the central area has been occupied by trees, it often may still be plainly traced.

SUMMARY.

In the filling-up of ponds, the activity of vegetation is in cases second to the physical factors of erosion and deposit. In open pools, anchored plants with floating leaves are often confined to a zone somewhat separated from the shore, their approach to the shore line being prevented by silt which is swept in, especially where the latter is shifted by wavelets. The physical factors in that zone thus exclude the organic. Plants of the shore line in such cases have running stems similar to those of sand binders, which enable them to escape death by burial.

The vegetation of the large open morainal pool, though undrained, may be purely hydrophilous. About the time of the formation of the floating mat the conditions appear to become xerophytic.

The marginal ditch which surrounds pond islands and atolls is in this region, at least, formed only in the woods, where a

dense felt of humus vegetation protects the ground from erosion. Fallen leaves and other organic materials swept from the forest floor into the edge of the pool tend to smother the vegetation which might grow there, and thus is produced a belt of open water, surrounding an island, or if the pond is larger a ring of vegetation.

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